

# THE REPRODUCTIVE MORPHOLOGY OF *PLATOMA CYCLOCOLPUM* (NEMASTOMATACEAE, GIGARTINALES) FROM GRAN CANARIA, CANARY ISLANDS

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**ABSTRACT** - Nine species currently included in the marine red algal genus *Platoma* (Nemastomataceae, Rhodophyta), which is typified by *P. cyclocolpum* (Montagne) Schmitz described by J.F.C. Montagne (as *Halymenia cyclocolpa*) in the early part of the last century from Tenerife, Canary Islands. Recently collected plants of *Platoma cyclocolpum* from another of the Canary Islands, Gran Canaria, are similar in morphology and reproduction to type material of *Halymenia cyclocolpa* Montagne, for which a lectotype is selected. Connecting filaments of *P. cyclocolpum* arise from subsidiary auxiliary cells fused or connected with fertilized carpogonia in the same manner as found in *Schizymenia*. These specimens and Montagne's material have large intercalary gland cells in the cortical fascicles. The other eight known species of *Platoma* and some other members of the Nemastomataceae require reinvestigation to establish their generic and familial relationships, but it is clear that *Platoma*, *Schizymenia* and *Titanophora* are more closely related to each other than they are to the remaining genera of the Nemastomataceae and should probably be referred to a separate family. The new combinations *Tsengia lancifolia* (Okamura) comb. nov. (basionym: *Nemastoma lancifolium* Okamura) from Japan and *Tsengia pulchra* (Bardseth) comb. nov. (basionym: *Nemastoma pulchrum* Bardseth) from Tristan da Cunha are proposed. Carpospores of Gran Canarian *P. cyclocolpum* developed into coherent crustose plants without gland cells; these superficially resemble the *Haematocelis*-phase of *Schizymenia dubyi* (Chauvin ex Duby) J. Agardh, but lack the refractive cell inclusions and secondary pit-connections between cells of adjacent perithallial filaments described for this phase. The *Platoma* crustose phase did not form erect axes and no sporangial reproduction took place under a wide range of environmental conditions.

**RÉSUMÉ**- Neuf espèces ont été couramment incluses dans le genre marin d'algue rouge *Platoma* (Nemastomataceae, Rhodophyta), qui est typifié par *P. cyclocolpum* (Montagne) Schmitz décrit par J.F.C. Montagne (comme *Halymenia cyclocolpa*) au début du siècle dernier de Tenerife, aux Iles Canaries. Récemment, des thalles du *Platoma cyclocolpum* récoltés sur une autre île des Canaries, Grande Canarie, sont semblables par leur morphologie et leur reproduction au matériel type de *Halymenia cyclocolpa* Montagne, dont un lectotype a été sélectionné. Les filaments connecteurs de

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*P. cyclocolpum* naissent de cellules auxiliaires subsidiaires après fusion ou connection de celles-ci avec le carpogone fécondé, de façon identique à ce qui a été trouvé chez *Schizymenia*. Ces spécimens et le matériel de Montagne ont de grosses cellules glandulaires intercalaires dans les faisceaux corticaux. Les huit autres espèces connues de *Platoma* ainsi que d'autres membres de Nemastomataceae nécessitent des recherches ultérieures afin d'établir leurs parentés au niveau générique et familial; cependant, il est clair que les genres *Platoma*, *Schizymenia* et *Titanophora* ont entre eux des rapports plus étroits qu'avec les autres genres de Nemastomataceae et qu'ils devraient probablement être rattachés à une famille différente. Les nouvelles combinaisons *Tsengia lancifolia* (Okamura) comb. nov. (basionym: *Nemastoma lancifolium* Okamura) du Japon, et *Tsengia pulchra* (Baardseth) comb. nov. (basionym: *Nemastoma pulchrum* Baardseth) de Tristan de Cunha sont proposées. Les carpospores du *P. cyclocolpum* de Grande Canarie se sont développés en croûtes cohérentes sans cellules glandulaires; superficiellement ils ressemblent à la génération *Haematocelis* du *Schizymenia dubyi* (Chauvin ex Duby) J. Agardh, mais leurs cellules ne présentent pas les inclusions réfringentes ni les synapses secondaires entre les cellules adjacentes des filaments du périthalle, qui ont été observée dans cette génération. La génération encroûtante, cultivée sous des conditions variées de l'environnement, n'a produit ni axes dressés, ni sporocystes.

Key Words: Gigartinales, Nemastomataceae, *Platoma*, Rhodophyta, *Tsengia*.

## INTRODUCTION

The red algal family Nemastomataceae<sup>2</sup> (J. Agardh) Schmitz in Engler (1892, p. 22 "Nemastomaceae"), also known as the Gymnophloeaceae Kützinger (1843, p. 389 "Gymnophlaeaceae"), currently includes seven genera (Womersley & Kraft, 1994): *Nemastoma* J. Agardh (1842, p. 89), *Schizymenia* J. Agardh (1851, p. 169), *Platoma* Schousboe ex Schmitz (1894, p. 627), *Predaea* G. De Toni (1936, p. 5), *Titanophora* J. Feldmann (1942, p. 111), *Tsengia* K. C. Fan et Y. P. Fan (1962, p. 191) and *Adelophycus* Kraft in Womersley & Kraft (1994, p. 146)<sup>3</sup>. These genera are characterised by various combinations of vegetative and reproductive features, but in most species ascribed to the family details of the female reproductive structures, post-fertilization development, and the vegetative and reproductive features of tetrasporophytes are required, particularly for the generatypes. For example, little is known of post-fertilization development in the type species of *Titanophora*, *T. pikeana* (Dickie) J. Feldmann, and in several genera tetrasporophytes are still unknown.

The genus *Platoma*<sup>4</sup> is one such genus and currently includes nine species: 1) *P. cyclocolpum* (Montagne) Schmitz (1894, p. 627 as *cyclocolpa*), the type species; 2)

<sup>2</sup> The name Nemastomataceae is not included in the *nomina familiarum algarum conservanda* listed in the current *International Code of Botanical Nomenclature* (Greuter 1988, p. 90), but its conservation against Gymnophloeaceae has been proposed (see Silva, 1993, p. 708).

<sup>3</sup> *Adelophycus* is a substitute name for *Adelophyton* Kraft (1975, p. 280) non *Adelophyton* Renault (1901, p. 424).

<sup>4</sup> Athanasiadis (1988, p. 31) regarded *Platoma* as neuter in gender, although it is generally considered to be feminine (see the discussion in Norris & Bucher 1977, p. 161, who concluded that traditional feminine usage should be maintained). It is relevant, however, to note that Montagne (1841, p. 163) treated the name as neuter. Generic names of plants derived from Greek ending in -

*P. marginiferum* (J. Agardh) Batters (1902, p. 94 as *marginifera*); 3) *P. incrassatum* Schousboe ex De Toni (1905, p. 1646 as *incrassata*); 4) *P. tenue* Howe et Taylor (1931, p. 32 as *tenuis*); 5) *P. izunosimense* Segawa (1938, p. 143 as *izunosimensis*); 6) *P. fanii* Dawson (1961, p. 197); 7) *P. abbotianum* J. N. Norris et Bucher (1977, p. 157 as *abbotiana*); 8) *P. foliosum* Womersley et Kraft (1994, p. 152 as *foliosa*); and 9) *P. australicum* Womersley et Kraft (1994, p. 152 as *australica*). The alga long known as *Platoma bairdii* (Farlow) Kuckuck (1912, p. 202) was transferred to *Tsengia* by Fan & Fan (1962, p. 191), a proposal that seems largely to have been overlooked.

The post-fertilization development of *Platoma cyclocolpum* (as *Nemastoma cervicorne* J. Agardh) was described by Berthold (1884, pp. 12, 22, pl. 6, figs 2, 3, 5, 8) on the basis of material from Pozzuoli, Bay of Naples, Italy. He found that the fertilized carpogonium first establishes a union with proximate subsidiary auxiliary cells ("sterilen Auxiliarzelle") prior to the formation of connecting filaments, and that gonimoblasts develop from an auxiliary cell fused with a connecting filament.<sup>5</sup> This pattern is similar to that described subsequently for the type species of *Schizymenia*, *S. dubyi* (Chauvin ex Duby) J. Agardh, by Ardré (1980). Berthold (*loc. cit.*), however, makes no mention of gland cells. Feldmann (1942, p. 106) later adopted the absence of gland cells ("cellules sécrétrices") as a critical feature of *Platoma* and thereafter the presence or absence of such cells was considered an important taxonomic feature at the generic level within the Nemastomataceae (e.g., Kylin, 1956; Dawson, 1961; Fan & Fan, 1962; Kraft & John, 1976; Dixon & Irvine, 1977; Womersley & Kraft, 1994). The description by Ardré (1980, p. 125, pl. 7, figs 65-67) of what appeared to be intercalary gland cells in the cortical fascicles of the type specimen of *Halymenia cyclocolpa* Montagne (the basionym of *P. cyclocolpum*) from Tenerife, Canary Islands (herb. Montagne, Muséum National d'Histoire Naturelle, Paris, PC) largely went unnoticed and *Platoma* continued to be distinguished principally on the basis of the presence or absence of gland cells (e.g., Womersley & Kraft, 1994).

An assessment of the status of *Platoma* thus requires critical study of the generic type, *P. cyclocolpum*. In the present study the vegetative and reproductive features of this species are reassessed on the basis of material recently collected from Gran Canaria, Canary Islands.

## MATERIALS AND METHODS

Plants were collected in the intertidal at Arinaga (27.50°N; 15.20°W), on the east coast of Gran Canaria, Canary Is. on 7 October 1993, and were transported live to University College, Galway, Ireland. Some were fixed in 4% Formalin in seawater and others were dried as herbarium specimens. Released carpospores were inoculated, by means of finely-drawn glass capillary pipettes, into drops of Von Stosch-enriched

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ma ( $\mu\alpha$ ) should, if only for the sake of consistency, be now be treated as neuter and this includes both *Nemastoma* and *Platoma*.

<sup>5</sup> The term « subsidiary auxiliary cell » is adopted here instead of « sterilen Auxiliarzelle » to distinguish these cells from the more usual type of auxiliary cell (see p. 208 of the Discussion).

seawater medium (25% strength; compounded according to Guiry & Cunningham, 1984) on cover slips (22 x 22 mm) or half-slides (25 x 37 mm) in culture dishes (70 x 50 mm). The next day, 120-150 ml of medium were added to each dish. Sporelings were initially grown at 20°C, 16:8 h LD (light:dark cycle), 12-14  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . Cultures were transferred to various combinations of daylength and temperature: 25°C, 8:16 h LD; 20°C, 8:16 h LD, 15°C, 16:8 h LD, and 15°C, 8:16 h LD, as necessary. Culture media and dishes were changed every two weeks.

The type material of *Halymenia cyclocolpa* Montagne was obtained on loan from herbarium Montagne, Muséum National d'Histoire Naturelle, Paris (PC). Periclinial, longitudinal and transverse sections were made by hand using a double-edged razor blade and pith stick, and stained with a mixture of Gurr's cotton blue-lactophenol (BDH Chemicals Ltd, Poole, Dorset, U.K.)/glycerol (1:1) and mounted in glycerol or 60% Karo<sup>®</sup> corn syrup (with added sugar).

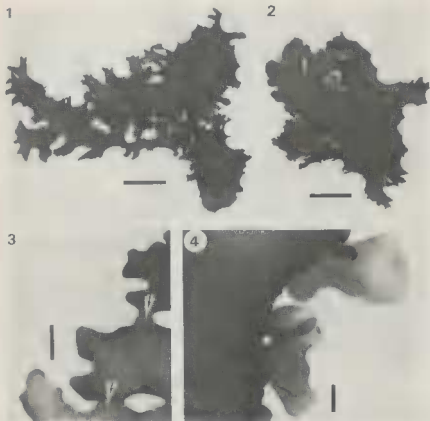
Voucher specimens and slides are deposited in the Phycological Herbarium, University College, Galway, Ireland (GALW), and in the Herbarium of the Graduate School of Science, Hokkaido University, Sapporo, Japan (SAP).

## OBSERVATIONS

### *Vegetative morphology of gametophytes*

In lower intertidal pools at Arinaga, Gran Canaria, gametophytes grow on rock in low light conditions beneath overhangs. Decumbent thalli arise singly from a discoid basal attachment structure, are brownish to liver-red in colour, fleshy, slippery but firm in consistency, to 50 mm long and to 60 mm broad. Stipes are absent. Blades spread decumbently over the substratum, sometimes become imbricate, are 0.3-0.7 mm thick in the terminal portions and 1.2-2.8 mm thick at the proximal portion. Branching is irregular with rounded bifurcations 2-3 mm broad at the apices (Figs 1, 2). The margins of adjacent branches often fuse with one another (Fig. 3) and adventitious proliferations arise from injured (perhaps grazed) thallus margins (Fig. 4). Plants adhere firmly to paper when dried.

Gametophytes are multiaxial (Figs 5, 6). The medulla is composed of loosely arranged, irregularly sparingly branched filaments which consist of more or less colourless, elongated cells, 7.5-12.5  $\mu\text{m}$  wide and 100-450  $\mu\text{m}$  long. At the surfaces of the thallus, filaments become organised into radially oriented fascicles 10-14 cells deep and 4-8 times dichotomously branched; the inner cells of the fascicles are obovate to elliptical and 10-25  $\mu\text{m}$  wide and 25-40  $\mu\text{m}$  broad and become progressively smaller outwards; cells at dichotomies are frequently cuneate. Surface cells are elliptical and 3.0-4.5  $\mu\text{m}$  in diameter. Secondary pit-connections do not occur between any of the medullary and cortical cells. Adventitious rhizoidal filaments are formed from cortical cells; these filaments are well developed and frequently transverse the thallus from cortex to cortex. Vegetative hairs are formed on some of the outermost cells of the cortex. Intercalary gland cells are borne frequently on cortical filaments (Figs 5-8) and sometimes on medullary filaments (Fig. 6); the gland cells are translucent and refractive in living material (Figs 5, 7), but become dense, granular and yellowish in

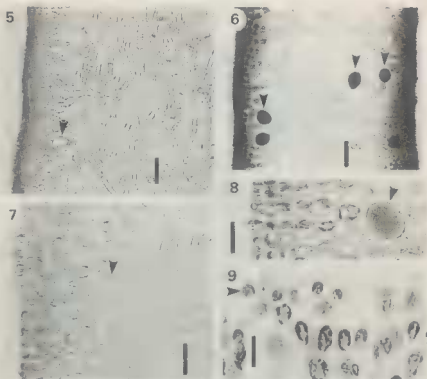


Figs. 1-4: *Platoma cyclocolpum*, Gran Canaria, Canary Is. (7.x.1993). Figs. 1, 2. Habit of voucher herbarium specimens (1, SAP 059805; 2, GALW 008759). Fig. 3. Upper margin of a Formalin/seawater-preserved specimen; arrows indicate fused portions of branches. Fig. 4. Adventitious proliferations from damaged (by grazing?) margin of a Formalin/seawater-preserved specimen. Scale bars represent: Figs 1, 2, 1 cm; Figs 3, 4, 1 mm.

Formalin/seawater-preserved material (Fig. 8). They are spherical, ellipsoidal, or ovoid in shape and the larger ones are 25-40  $\mu\text{m}$  in diameter and 25-50  $\mu\text{m}$  in length and stain deeply with cotton blue (Fig. 6).

### *Reproductive morphology*

Both sexes are found on each plant. Spermatangial sori are small and are formed on the upper surface, mostly near the margins. Spermatangia (3-4  $\mu\text{m}$  wide and 4-5  $\mu\text{m}$  long) are subspherical and are cut off in pairs from the outermost cortical cells



Figs. 5-9: *Platoma cyclocolpum*, Gran Canaria, Canary Is. (7.x.1993). Figs 5-8. Longitudinal sections of central portions of thalli, showing multiaxial structure and intercalary gland cells (arrowheads): Figs. 5, 7, living material; Figs 6, 8, Formalin/seawater-preserved material (6, stained with cotton blue-lactophenol; 8, not stained). Fig. 9. Transverse section of the upper portion of thallus which form an outermost spermatangial layer (arrowhead). Scale bars represent: Fig. 5, 50  $\mu$ m; Fig. 6, 100  $\mu$ m; Fig. 7, 30  $\mu$ m; Fig. 8, 20  $\mu$ m; Fig. 9, 10  $\mu$ m.

(Fig. 9). Outwardly directed carpogonial branches are found throughout the plants except at the extreme base; they are three-celled and are formed singly from the basal cell (the supporting cell) of cortical fascicles in the inner cortex (Fig. 10). The carpogonial branch and its supporting cell stain darkly with cotton blue and thus are easily detected. The carpogonium is conical, 4.5-6.0  $\mu$ m wide, narrowing to a long trichogyne, 2.5-4.0  $\mu$ m in width. The hypogynous cell is hemispherical to barrel-shaped, 7.5-11.0  $\mu$ m wide. The basal cell is barrel-shaped, 10-17  $\mu$ m wide. The two to three proximal cells of cortical fascicles borne on the supporting cell also stain darkly with cotton blue (Figs 10-12), and sometimes four such cells stain darkly. After presumed fertilization, the carpogonium connects with one of the darkly staining proximal cells which then cuts off a connecting-filament initial (Fig. 11). The

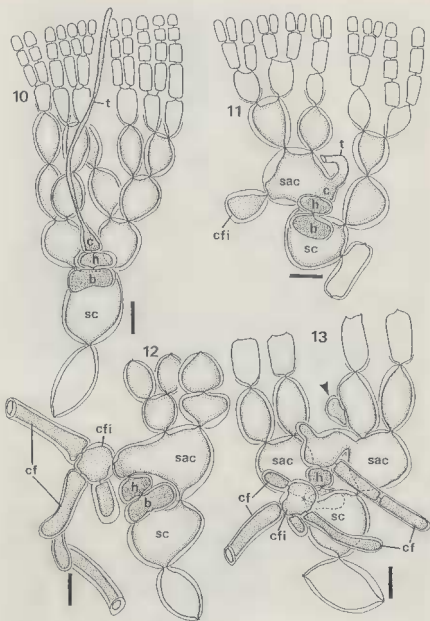
connecting-filament initial produces several connecting filaments in different directions (Fig. 12). Another darkly staining proximal cell becomes connected to the carpogonium by a secondary pit-connection and forms a connecting-filament initial which also produces several, septate connecting filaments 3-6  $\mu\text{m}$  in diameter (Fig. 13). Additionally, one of supraproximal cells may produce a connecting-filament initial (Fig. 13). The darkly staining cells that connect with the carpogonium by direct fusion or via secondary pit-connections are essentially subsidiary auxiliary cells. During this development the trichogyne disappears and shed trichogyne-like structures are sometimes found near the female reproductive apparatus. Other darkly staining cells may produce connecting filaments, but at this stage so many cells are involved that resolution of every detail is impossible.

Connecting filaments fuse with auxiliary cells, which are transformed from the basal cells of cortical fascicles other than those that bear the carpogonial branches, and grow onwards to another auxiliary cell (Figs 14-16). The auxiliary cells that have fused with connecting filaments produce an outwardly directed gonimoblast initial (Fig. 14). The gonimoblast initial divides to form several cells which again branch repeatedly (Figs 15, 16). As the carposporophyte develops, the proximal one or two cells of the cortical fascicles on the auxiliary cell become larger, elongate and arch around the carposporophyte (Fig. 16), and the basal cell of the carposporophyte (the gonimoblast initial) becomes columnar (Fig. 16). All cells of the carposporophyte, except for the basal cell, develop into spherical carposporangia 15-20  $\mu\text{m}$  in diameter. Mature carposporophytes are subspherical, 150-200  $\mu\text{m}$  in diameter and are embedded in the cortex (Fig. 17). Carpospores are released through a gap in the cortical fascicles and no true ostiole is developed. The surface of the thallus in the area of carposporophyte formation does not form a depression.

### *Typification of Halymenia cyclocolpa Montagne*

The type material of *Halymenia cyclocolpa* in Herb. Montagne (PC) is labelled: "*Halymenia multifida* Montag./ *Platoma* Schousb./ voir l'herb. de M. Webb/ Canaria, Teneriffe". The sheet includes a contemporary drawing (labelled "*H. multifida*" and "*Halymenia cyclocolpa*" and two specimens in an envelope: one is mounted on mica (Fig. 18) and the other is in a smaller envelope (Fig. 19). Both are fragments of foliose thalli. Longitudinal sections of small portions of these specimens were made. The fragment on mica is very faded and has a loosely arranged filamentous medulla corresponding with the drawing: the cortical cells are arranged in fascicles (Fig. 20). Gland cells are intercalary on cortical fascicles and outwardly developing gonimoblasts are present in the cortex (Fig. 20). The other specimen, however, has retained its red colour and has a tightly packed medulla and cortex, but its carposporophytes are sunken in the medulla (Fig. 21), there are sterile cells separating groups of carposporangia, and the blade is swollen in the area of carposporangial formation. The cortex is not fasciculate and just below it there is a layer of spherical cells. There are

<sup>6</sup> It appears that Montagne may initially have intended to use Schousboe's unpublished specific epithet "*multifida*" but subsequently changed his mind and employed "*cyclocolpa*".



thus two quite different plants included in the type material and one of these clearly has features that are not those of an alga referable to the Nemastomataceae.

As to type materials, therefore, *Halymenia cyclocolpa* Montagne seems to be heterogeneous. In his description, Montagne (1841, p. 163) refers to two collections: the first was material collected by P. B. Webb "in littore Teneriffae" and the other collected at Tangier by P.-K.-A. Schousboe<sup>7</sup>. In his description, however, it is quite clear that Montagne was describing a plant very similar to that on mica: "*Radix callus exiguus. Frons carnosio-membranacea, valde gelatinosa, e basi attenuata filiformi brevissima mox in laminam expansa circumscriptione ovalem aut semiorbicularem... planam, irregulariter subdichotomam...*". The accompanying drawing (PC-MS 446-278) is clearly of the specimen on mica as it shows fascicles of cortical cells and a mature carposporophyte in the cortex. As the specimen on mica (Fig. 18) accords with the description we hereby select it as the lectotype of *Halymenia cyclocolpa* Montagne (PC-MA 14293).

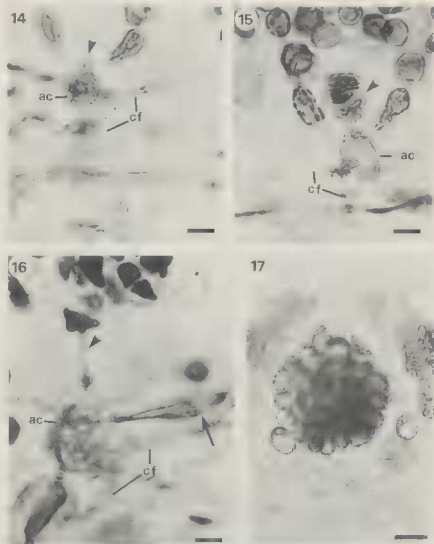
### *Carpospore development*

Liberated carpospores were spherical, light red in colour and 12.5-20.0 µm in diameter (Figs 22-24); they attached firmly to the substratum and divided into two to four cells within 2 d (Figs 25, 26) at 20°C, 16:8 h LD. Various germling shapes were produced: from compact crusts to creeping, loosely aggregated filaments with many intermediates (Figs 27-30). These germlings grew rapidly and reached 700-1000 µm in diameter after 4 weeks (Figs 31, 32). These four-week-old plants were divided into four groups of which three were transferred to 15°C, 8:16 h, 15°C, 16:8 h, and 20°C, 8:16 h. One group was maintained at 20°C, 16:8 h as a control. Further plants were transferred to 25°C, 8:16 h about two months later.

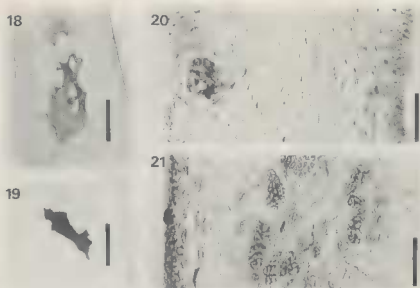
Plants grew well at all these culture conditions and the majority of creeping, loosely aggregated filamentous germlings gave rise to tightly coherent crusts, but some remained loosely aggregated (Fig. 33), and these latter plants showed an anti-clockwise

Figs. 10-13: *Platoma cyclocolpum*, Gran Canaria, Canary Is. (7.x.1993). All transverse sections of Formalin/seawater-preserved specimens and stained with cotton blue/lactophenol. Peripheral portions of darkly staining cells other than carpogonial branches (the supporting cell and proximal two or three layers of the cortical fascicles borne on the former) are dotted. Fig. 10. Three-celled carpogonial branch. Fig. 11. Fusion between the carpogonium and one of darkly staining cells which is cutting off ■ connecting-filament initial and thus is confirmed as a subsidiary auxiliary cell. Fig. 12. Three connecting filaments developing from the connecting-filament initial; one cortical fascicle is not shown. Fig. 13. More advanced stage of the production of connecting filaments: a further subsidiary auxiliary cell united with the carpogonium by a secondary pit-connection is forming four connecting filaments. An arrowhead indicates a probable connecting-filament initial. b, basal cell; c, carpogonium; cf, connecting filament; cfi, connecting-filament initial; h, hypogynous cell; sac, subsidiary auxiliary cell; sc, supporting cell; t, trichogyne. Scale bars represent 10 µm.

<sup>7</sup> P.-K.-A. Schousboe in an unpublished manuscript (see Bornet 1892, p. 165-6) named this material ■ the type of ■ new genus *Platoma* (as *Platoma multifida* Schousboe, a *nomen nudum*); the genus name *Platoma* was a *nomen nudum* until Schmutz (1894, p. 627) validated it.



Figs. 14-17: *Platoma cyclocolpum*, Gran Canaria, Canary Is. (7.x.1993). All transverse sections: Figs. 14-16, Formalin/seawater-preserved specimens and stained with cotton blue-lactophenol; Fig. 17, living material. Fig. 14. Auxiliary cell united with a connecting filament bearing gonimoblast initial (arrowhead). Fig. 15. Three gonimoblast cells developing from the auxiliary cell. Fig. 16. More advanced stage of gonimoblast development; arrowhead indicates an elongated basal cell, arrow indicates an elongated proximal cell of the cortical fascicle arching around the carposporophyte. Fig. 17. Mature carposporophyte. ac, auxiliary cell. cf, connecting filament; Scale bars represent: Figs. 14-16, 10  $\mu$ m; Fig. 17, 30  $\mu$ m.

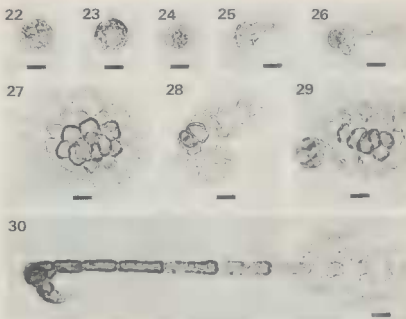


Figs 19-21. Type material of *Halymenia cyclocolpa* Montagne deposited in PC. Fig. 18. Lectotype specimen designated in this paper and mounted on mica (PC-MA 14293). Fig. 19. Fragment of another foliose specimen in a small paper envelope. Fig. 20. Longitudinal section of the lectotype. Note loosely arranged cortical fascicles and outwardly directed gonimoblasts within the cortex. Fig. 21. Longitudinal section of the specimen shown in Fig. 19. Note tightly packed cortex and deeply sunken gonimoblasts in the medulla. Scale bars represent: Figs 18, 19, 1 cm; Figs 20, 21, 50  $\mu$ m.

growth pattern. Three-month-old plants were up to 5 mm in diameter and 6-7 layers in thickness (a single-layered hypothallium and a 5-6-layered perithallium) (Fig. 34). At eight months plants at 25°C, 8:16 h, were 13 mm in diameter and 7-8 layers in maximum thickness. These plants had neither gland cells nor refractive cell inclusions, although some larger, more densely staining terminal cells were observed. No secondary pit-connections were found between any of the cells in either the hypothallium or the perithallium. No reproductive structures were formed at any of the daylength and temperature combinations. Rhizoids formed from the hypothallial cells in areas where the crustose plants became detached, and these eventually reattached the plants.

## DISCUSSION

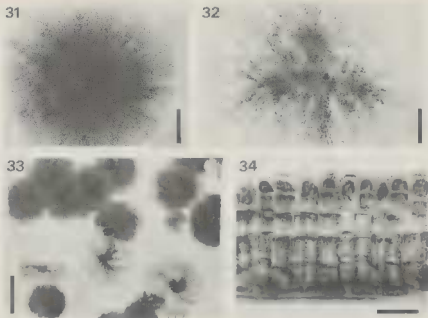
The type material of *Halymenia cyclocolpa* includes two disparate elements: a portion of a specimen on mica and a fragment in a small paper envelope. The material on mica agrees with the original description and with pencilled drawings



Figs 22-30. *Platoma cyclocolpum*, Gran Canaria, Canary Is. (7.x.1993). All living material. Figs 22-24. Released carpospores. Figs 25, 26. Two-day-old carposporelings at 20°C, 16:8 h LD. Figs 27-30. Seven-day-old carposporelings at 20°C, 16:8 h LD. Scale bar represents 10 µm.

accompanying the type sheet and it is herewith designated the lectotype of *Halymenia cyclocolpa* Montagne (1841, p. 163). Our specimens collected from Gran Canaria are identical to the lectotype specimen of *Halymenia cyclocolpa* in thallus structure, position of gland cells, and location of the developing gonimoblasts. Furthermore, the fragment on mica is very similar in gross morphology to parts of our specimens and corresponds in most respects with the original description. The identity of the other specimen is doubtful but it may represent a foliose alga of the family Kallymeniaceae.

Our observations of female reproductive structures and the post-fertilization development of *Platoma cyclocolpum* from the Canary Is. may be summarised as follows: 1) a three-celled carpogonial branch is formed on the basal cell (the supporting cell) of the cortical fascicles; 2) the fertilized carpogonium first connects with nearby subsidiary auxiliary cells, which are several nearby cells of the cortical fascicles formed on the supporting cell; 3) a number of connecting filaments are cut off from these subsidiary auxiliary cells and fuse with auxiliary cells, which are situated in the corresponding position to the supporting cell; 4) auxiliary cells that have fused with a connecting filament cut off a gonimoblast initial outwards; 5) the gonimoblast initial is divided into several cells that become repeatedly branched and form a



Figs 31-34. *Platoma cyclocolpum*, Gran Canaria, Canary Is. (7.x.1993). Living material unless otherwise indicated. Figs 31, 32. Four-week-old tetrasporophytes cultured at 20°C, 16:8 h LD: tightly coherent crustose plant (Fig. 31) and loosely aggregated plant (Fig. 32). Fig. 33. Three-month-old tetrasporophytes (two months after transfer from 20°C, 16:8 h LD to 20°C, 8:16 h LD). Fig. 34. Tangential section of a three-month-old crustose tetrasporophyte (stained with cotton blue-lactophenol). Scale bars represent: Figs 31, 32, 200 µm; Fig. 33, 4 µm; Fig. 34, 20 µm.

carposporophyte; 6) almost all cells of the carposporophyte are transformed into carposporangia and cortical fascicles on the auxiliary cell develop into an involucre-like structure; 7) carpospores are released through a gap in the cortical fascicles. These features accord in most respects with Berthold's (1884, pp. 12, 22, pl. 6, figs 2, 3, 5, 8 as *Nemastoma cervicorne*) description of material from the Gulf of Naples. However, his illustrations (Berthold, 1884, pl. 4, figs 1, 2) indicate plants quite different in gross morphology to our Gran Canarian specimens, as they are foliose, profusely and regularly branched plants in contrast to our sparingly and irregularly branched, decumbent, imbricate plants. Further study is thus needed to establish whether *Platoma cyclocolpum* and *Nemastoma cervicorne* are indeed conspecific as concluded by various authors. Athanasiadis (1987, p. 53) recently reported *Platoma cyclocolpum* from the Aegean Sea, but his material apparently lacks intercalary gland cells. The specific and generic status of this alga require further studies of its female reproductive structure and post-fertilization development.

Of the species currently included in *Platoma*, only two species, recently described from southern Australia, *P. australicum* and *P. foliosum*, are known to possess darkly staining cells adjacent to the carpogonial branch (Womersley & Kraft, 1994, p. 152, 153). Although Womersley & Kraft (*loc. cit.*) did not observe any connections between the carpogonium and these darkly staining cells, they may be subsidiary auxiliary cells as found in *P. cyclocolpum*. Subsidiary auxiliary cells have not been reported for any of the other putative species of *Platoma*. Post-fertilization development of these species thus requires critical investigation in order to clarify their generic status. Our observations on the post-fertilization development of *P. cyclocolpum* indicate that carpogonial branches and advanced stages forming many connecting filaments are more frequent than early post-fertilization development stages (primary fusion and secondary connection between the carpogonium and subsidiary auxiliary cells), which strongly suggests that post-fertilization development proceeds very rapidly. This may be the reason why there are very few details of post-fertilization development in other species of *Platoma*.

Although the genus *Platoma* is characterised by the above-mentioned reproductive features, the frequent occurrence of intercalary gland cells in the cortical fascicles is also a critical diagnostic feature; such intercalary gland cells have not been reported for other species of *Platoma*. However, *P. izunosimense* from Japan may also have such gland cells. Segawa (1938, p. 144) does not specifically mention gland cells in his descriptions; however, he does say: "In almost all the material, very frequently, ovate and brilliantly yellowish cells are seen in the cortical layer. They are the innermost cells of the cortical cell-series. Though there is some question, they may be auxiliary cell." These intercalary, ovate and brilliantly yellowish cells are probably gland cells as those of *P. cyclocolpum* also become yellowish when preserved in formalin/seawater. Such yellowish, granular, intercalary gland cells occur in *Titanophora submarina* Bucher et Norris (1992). However, Womersley & Kraft (1994), describing two new Australian species of *Platoma* that lack gland cells, claimed, in agreement presumably with Feldmann (1942), Kylin (1956) and others, that the absence of gland cells was an important generic feature of *Platoma*. Further study of these and other species is now needed to establish whether or not gland cells are a specific or a generic character in the Nemastomataceae, as although some species of *Titanophora* have gland cells, others do not (Bucher & Norris, 1992, table 2). In *Schizymenia dubyi* from the British Isles, Dixon & Irvine (1977, p. 177) found that "...only a minority of specimens" have gland cells, an observation disputed by Ardre (1980) and DeCew *et al.* (1992) who found them to be abundant in all specimens examined. Nevertheless, it is clear that gland cells are in certain circumstances difficult to observe and conclusions based on their presence or absence as a character must be treated with caution.

Critical taxonomic features of seven known genera of the family Nemastomataceae are given in Table I. A particular problem exists with regard to connecting filaments of the generitype of *Nemastoma*, *N. dichotomum* J. Agardh: Berthold (1884, pl. 6, figs 9-11, 14) clearly shows connecting filaments fusing with auxiliary cells and issuing gonimoblasts; Athanasiadis (1988), on the other hand, reports that gonimoblasts directly develop from an auxiliary cell that is not fused with

Table 1. A comparison of morphological and reproductive features of the genera of the Nemastomataceae

	<i>Adelophycus</i>	<i>Nemastoma</i>	<i>Platoma</i>	<i>Predaea</i>	<i>Schizymenia</i>	<i>Titanophora</i>	<i>Tsengia</i>
Gland cells	terminal	terminal	intercalary	intercalary or absent	terminal	intercalary	absent
Calcification	absent	absent	absent	absent	absent	present	absent
Position of supporting cell	cortical fascicle	adventitious filament	cortical fascicle	cortical fascicle	cortical fascicle	cortical fascicle	cortical fascicle
Sterile-cell branchlet or carpogonial branch?	no	no	no	yes/no	yes	no	no
Position of auxiliary cell	adventitious filament	adventitious filament	cortical fascicle	cortical fascicle	cortical fascicle	cortical fascicle	cortical fascicle
Subsidiary auxiliary cells?	no	no	yes	no	yes	probably	no
Origin of gonimoblast	connecting filament	connecting filament	auxiliary cell	auxiliary cell or connecting filament	auxiliary cell	auxiliary cell	auxiliary cell
Direction of gonimoblast development	inwards	outwards	outwards	outwards	outwards	outwards	outwards
Nutritive cells?	no	no	no	yes	no	no	no
Tetrasporophyte	unknown	unknown	crustose	crustose or filamentous	crustose	unknown	cruciate
Secondary pit connections in crustose phase	not applicable	not applicable	absent	absent	present	not applicable	not applicable
Cleavage of tetrasporangia	unknown	unknown	unknown	zonate	zonate	unknown	cruciate
Reference(s)	Kraft 1975	Berthold 1884; Athanasiadis 1988	present paper	Kraft & Abbott 1971; Kraft 1984; Millar & Guiry 1989	Ardre 1980	Mshigeni & Papenfuss 1980; Bucher & Norris 1992	Fan & Fan 1962

a connecting filament and concludes that his material (from Sithonia, north Aegean Sea, Greece) may be apomictic. Further studies are required to clarify these observations.

*Platoma* and *Nemastoma* have been variously distinguished by previous investigators (Kylin, 1932, 1956; Feldmann, 1942; Kraft & John, 1976) but, in our opinion, can be most clearly separated by the position of supporting cell and auxiliary cell, the presence or absence of subsidiary auxiliary cells, and the origin of gonimoblasts as previously described by Berthold (1884, pp. 12, 22-23, pl. 6, figs 1-14). To these characters should be added one in relation to the position of formation of the gland cells. Contrary to the opinions of various authors (e.g., Feldmann, 1942; Kylin, 1956; Kraft & John, 1976) who doubt the occurrence of such cells in species of *Platoma*, the mode of origin (in terminal position in *Nemastoma* species and in intercalary position in *Platoma* species) is a valuable distinguishing character.

*Adelophycus* and *Nemastoma* are more closely related than previously appreciated (Table I). The former genus is characterised by the possession of adventitious auxiliary-cell-bearing rhizoidal filaments, although the supporting cells are intercalary on ordinary cortical fascicles (Kraft, 1975, as *Adelophyton*). *Nemastoma* has similar filaments, and the supporting cells are also intercalary on such filaments (Berthold, 1884; Athanasiadis, 1988). It should be stressed that adventitious rhizoidal filaments are also abundant in our material of *Platoma cyclocolpum* and transverse the thallus in a very characteristic manner, but are always sterile. These filaments are probably homologous with the reproductive rhizoidal filaments of *Adelophycus* and *Nemastoma*. The production of reproductive cells on such filaments may show the shift of reproductive ability from ordinary cortical fascicles to adventitious filaments (or from adventitious filaments to ordinary cortical fascicles), partially in *Adelophycus* and fully in *Nemastoma*.

The reproductive features of *Nemastoma* species other than *N. dichotomum* are poorly known and should be re-examined. *Nemastoma confusum* Kraft et D. John (1976) is apparently not a member of this genus, since its supporting cells and auxiliary cells are transformed from the basal cell of cortical fascicles and the gonimoblast is initiated directly from the auxiliary cell. These features and the intercalary position of its gland cells ally *Nemastoma confusum* with *Platoma cyclocolpum*. The mode of initiation of connecting filaments of *N. confusum*, however, needs to be clarified prior to any generic repositioning of this species. Carpogonial branches of *N. canariense* (Kützinger) J. Agardh are borne on a supporting cell that is intercalary on ordinary cortical fascicles (Børgesen, 1929, p. 11), suggesting that this species may be more closely related to *Adelophycus* than to *Nemastoma*.

Now that a more precise definition of *Platoma* is possible, it is clear that it is very closely related to *Schizymenia*. We consider that the presence of sterile branchlets on the carpogonial branches in *Schizymenia* and their absence in *Platoma* ■ sufficiently clear reproductive character to distinguish these genera. Additionally, the position of gland cells is different: terminal on cortical fascicles in *Schizymenia* and intercalary in the cortical fascicles of *Platoma* (Table I); shape differences may also be important as the gland cells of *Platoma cyclocolpum* are 1-2 longer than broad whilst those of *Schizymenia dubyi* are generally 2-4 times (Dixon & Irvine, 1977, p. 176; Ardré, 1980,

fig. 15). Other than the characters shown in Table I, some authors have adopted features such as the consistency of the erect thalli (coriaceous vs. mucilaginous; e.g., Dawson, 1961), and the position of the ostiole above each carposporophyte (depressed vs. not depressed; Womersley & Kraft, 1994). Neither of these criteria now seem particularly relevant in terms of the type species of the respective genera.

A heteromorphic-type life history (*Bonnemaïsonia hamifera*-type; Dixon 1982) is known in two species of *Schizymenia*, *S. dubyi* from Europe (Ardré, 1980) and Japan (Migita & Kawamura, 1980) and *S. pacifica* (Kylin) Kylin<sup>1</sup> from North America (DeCew *et al.*, 1992a). These species have crustose tetrasporophytes formerly referred to *Haematocelis rubens* J. Agardh. The *Haematocelis*-phase tetrasporophytes of *Schizymenia* are vegetatively characterised by the presence of secondary pit-connections between adjacent cells (Ardré, 1980), whereas crustose *P. cyclocolpum* plants derived from carpospores lack such connections. The *Haematocelis*-phase tetrasporophytes of *Schizymenia* are further characterised by the presence of refractive, spherical cell inclusions (Ardré, 1970, 1977; Cormaci *et al.*, 1976) which may be the result of special secondary metabolite synthesis. The supposed tetrasporophytes of *P. cyclocolpum*, however, do not produce such cell inclusions. Clearly, therefore, *Platoma cyclocolpum* and *Schizymenia dubyi* are sufficiently different in gametophytic and tetrasporophytic characters to be included in two separate genera.

Although foliose tetrasporophytes of *Schizymenia* species have been reported in Europe (e.g., Crouan & Crouan, 1867, fig. 92; Newton, 1931, p. 281), Japan (Okamura, 1933b) and Pacific North America (Abbott, 1967), these records are probably entirely due to misidentifications of similar blade-like algae. The European records were largely rejected by Ardré (1977) and Dixon & Irvine (1977) and those from Pacific North America by DeCew *et al.* (1992a). It is relevant in this regard to note that gland cells of *Schizymenia* species are sometimes divided or fractured zonately or irregularly in a similar manner to tetrasporangia in herbarium specimens as we have found in plants from Monterey, California (leg. M. D. Guiry, 13.vii.1976; GALW 002452; Masuda & Guiry, unpubl. obs.). Such divided or fractured gland cells are also reported for *Opuntiella californica* (Farlow) Kylin (DeCew *et al.*, 1992b), a species from the Pacific coast of North America, and may have been mistaken for tetrasporangia.

The genus *Predaea* is characterised by the production of small nutritive cells [originally termed "*cellules nourricières*" by Feldmann (1942, p. 109)] from cells adjacent to the auxiliary cell. The genus includes some 13 species (Millar & Guiry, 1989; Verlaque, 1990), and two groups of species are apparent: 1) those in which the gonimoblast originates from an auxiliary cell; 2) those in which the gonimoblast originates from a connecting filament at a point near that of its union with the auxiliary cell (Kraft & Abbott, 1971; Millar & Guiry, 1989). Although *Predaea ollivieri* J. Feldmann from the Mediterranean was described (Kraft & Abbott, 1971) as possessing both types of gonimoblast initiation, this observation was in error (Kraft in Athanasiadis, 1988, p. 30) being due to: "a mistake or the result of observations on

<sup>8</sup> DeCew *et al.* (1992a) all but conclude that there are no grounds upon which *S. pacifica* can be distinguished from *S. dubyi* and although plants may be larger in the Pacific, this is not reasonable grounds for species separation.

another species [*Predaea pusilla* (Berthold) J. Feldmann?] being mixed in the material examined". The taxonomic significance of two such types of gonimoblast initiation in a single genus now requires reinvestigation and a segregate genus may be necessary.

The post-fertilization development of *Titanophora*, which is characterised by having calcified thalli (Feldmann, 1942), is very poorly known. The "two to four large deeply-staining cells" reported by Mshigeni & Papenfuss (1980, p. 787) associated with the carpogonial branch of *T. weberae* Børgesen from Tanzania, are probably homologous with the subsidiary auxiliary cells of *Platoma* and *Schizymenia* and have been described as "subsidiary cells" by Bucher & Norris (1992). These cells have not been described for the genotype *T. pikeana* (Dickie) J. Feldmann. The development of an involucre around the carposporophytes of some species of *Titanophora* (Mshigeni & Papenfuss, 1980; Bucher & Norris, 1992) is very similar to that found in *Platoma cyclocolpum* but such an involucre seems to be absent in *Schizymenia dubyi*. In *Titanophora*, the possibility that calcification with aragonite is not the unifying character it is claimed to be should be examined.

Although the genus *Tsengia* was established by Fan & Fan in 1962, its existence was not widely realised until recently. It was originally characterised as: 1) lacking gland cells; 2) having an auxiliary cell transformed from the basal cell of cortical fascicles; 3) forming connecting filaments from the fertilized carpogonium; 4) having a carpogonium and trichogyne that lie at right angles to the first two cells of the carpogonial branch; and, 5) having a gonimoblast directly originating from auxiliary cells. Two species, *T. nakamurae* (Yendo) K. C. Fan et Y. P. Fan and *T. bairdii* (Parlow) K. C. Fan et Y. P. Fan were originally included in the genus (Fan & Fan, 1962). In addition to these diagnostic features, the occurrence of isomorphic gametophytes and tetrasporophytes is also considered to be a critical feature (Womersley & Kraft, 1994). This genus may ultimately accommodate further species presently placed in other genera of the Nemastomataceae. Womersley & Kraft (1994) recently proposed the transfer to *Tsengia* of three southern Australian species previously placed in *Nemastoma*.

Two further species can be added to these. *Nemastoma lancifolium* Okamura (1933a, p. 5) from Japan is clearly a species of *Tsengia*<sup>9</sup>. Kawashima (1957) reported its female reproductive structures and post-fertilization development as follows (translated from the Japanese): "Carpogonial branches with small carpogonia are usually three-celled and rarely two- or four-celled. Trichogynes are coiled near the proximal portion. After fertilization carpogonia enlarge and produce 2-4 protuberances from which septate or non-septate, branched connecting filaments arise. The connecting filaments contact with auxiliary cells, which are evident before union, growing towards other auxiliary cells and unite with them. Gonimoblasts develop from auxiliary cells." This species possesses isomorphic gametophytes and tetrasporophytes, and the tetrasporangia have cruciately arranged spores (Okamura 1933a; Kawashima 1957). Similarly, *Nemastoma pulchrum* Baardseth (1941, p. 65) described from Tristan

<sup>9</sup> *Tsengia lancifolia* (Okamura) Masuda et Guiry comb. nov. Basionym: *Nemastoma lancifolium* (as *lancifolia*) Okamura, *Icones of Japanese Algae* Vol. 7: 5, pl. 303, figs 1-3, 1933

Da Cunha is a species of *Tsengia*, as it has isomorphic gametophytes and tetrasporophytes<sup>10</sup>.

In conclusion, we are entirely in agreement with Womersley & Kraft (1994, p. 145) that the seven genera presently ascribed to the Nemastomataceae can be divided into two radically different groups: 1) the *Nemastoma* group comprising: *Nemastoma*, *Adelophycus*, *Tsengia* and *Predaea*, lacking subsidiary auxiliary cells (connecting filaments developing directly from fertilized carpogonia); and, 2) the *Schizymenia* group comprising *Schizymenia*, *Platoma*, and *Titanophora* having subsidiary auxiliary cells. These two groups may also differ in having filamentous, or loosely coherent, crustose tetrasporophytes in the *Nemastoma* group and strongly coherent, crustose tetrasporophytes in the *Schizymenia* group. It is probable that the two groups may ultimately be included in separate families, as also suggested by G.T. Kraft (pers. comm.).

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<sup>10</sup> *Tsengia pulchra* (Baardseth) Masuda et Guiry comb. nov. Basionym: *Nemastoma pulchrum* (as *pulchra*) Baardseth, *Res. Norweg. Sci. Exped. Tristan da Cunha* 9: 65, figs 32, 34 (A-C), 1941

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